THE JURASSIC *LITHOCODIUM AGGREGATUM-TROGLOTELLA INCRUSTANS* FORAMINIFERAL CONSORTIUM

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ABSTRACT. *Lithocodium aggregatum*, an enigmatic micro-encruster widespread in Mesozoic shallow marine carbonates, was considered to be a codiacean alga but can now be identified from Upper Jurassic examples as loftusiid foraminifer (Order Lituolida, Superfamily Loftusiacea). The microgranular wall may also contain detrital quartz, a feature which excludes any codiacean affinity. The complex, alveolar though imperforate, wall structure is identical to that of other loftusiid foraminifers; the only difference is the encrusting life habit of *Lithocodium*. The foraminifer is coiled in juvenile growth stages but subsequently developed irregular growth, making it possible for it to contribute to the formation of oncoids and reefal biotic crusts. The numerous alveolar structures, which are covered by only a very thin outer wall, suggest that these alveoli were containers for photoautotrophic symbionts. *Lithocodium* and *Bacinella* are not parts of one single organism, although phrenotheca-like structures crossing parts of the chambers partly resemble the latter. In the Upper Jurassic material, nearly every specimen of *Lithocodium* includes bubble-like structures, formerly interpreted as algal sporangia. These structures are identified here as the foraminifer *Troglotella incrustans*. During its later growth, *Troglotella* developed an irregular shape and grew into the alveoli of the *Lithocodium* walls. This may be interpreted as a commensal relationship, with *Troglotella* feeding on the carbohydrates synthesized by the *Lithocodium* symbionts.

THE encrusting microorganism *Lithocodium aggregatum* is widespread in Mesozoic shallow-water carbonates. It was first described from the Cretaceous of Iraq by Elliott (1956) who interpreted it as a codiacean alga, but later regarded it as a form of uncertain affinity ('*Lithocodium-Bacinella*, a very doubtful structure...', Elliott 1978, p. 438), and its systematic position is controversial. The common, though not obligate intergrowth with *Bacinella irregularis*, another enigmatic micro-encruster (Pl. 1, fig. 5), led to the assumption that both taxa represent a tissue differentiation of one single organism (Segonzac and Marin 1972; Banner *et al.* 1990) or different ecological varieties of one organism (Maurin *et al.* 1985), although these interpretations were mostly not followed by other authors. Leinfelder (1986), regarding the form as *incertae sedis*, discussed some similarities with hydrozoans, stromatoporoids or ancestral coralline algae (see below for further discussion). Based on rich new collections of Upper Jurassic material, we will demonstrate that *Lithocodium* shows all the features of a loftusiid foraminifer such as *Pseudocyclammina lituus*.

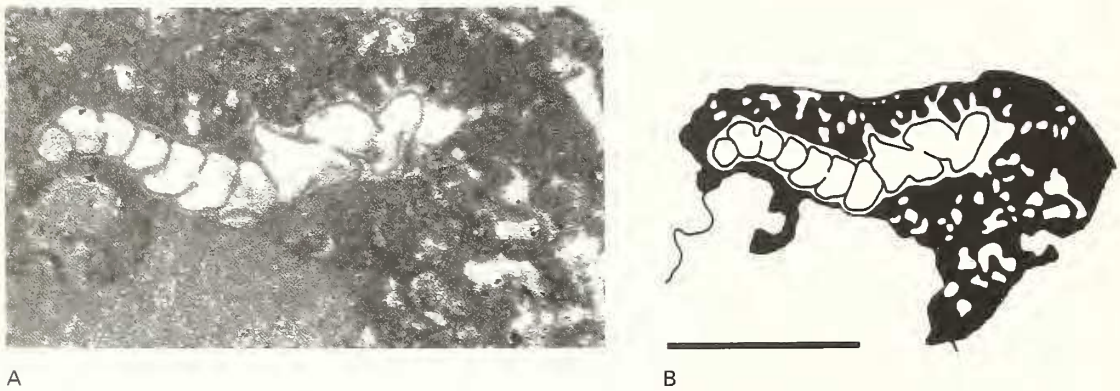
Lithocodium exhibits a basal cavity which, in the Upper Jurassic material, is often occupied by bubble-like structures (Text-fig. 1). In the algal model, these structures have been interpreted as sporangia (cf. Endo 1961). Leinfelder (1989), Leinfelder *et al.* (1993), and Schmid *et al.* (1993) showed that these bubble-like structures clearly represent a foraminifer (Text-fig. 2) which was provisionally termed *Bullopora* aff. *laevis*. This foraminifer, exhibiting a coelobitic life style, has now been identified as *Troglotella incrustans* Wernli and Fookes, 1992.

In the Triassic as well as in the Cretaceous, *Lithocodium* appears not to be associated with a coelobitic foraminifer. Instead, the basal cavity is empty or commonly occupied by *Bacinella* (Pl. 1, fig. 5), another enigmatic microencruster, in an intimate relationship which occurs only very rarely in the Upper Jurassic material.

Upper Jurassic *Lithocodium* is often a major contributor to the formation of oncoids as well as

[Palaeontology, Vol. 39, Part 1, 1996, pp. 21–52, 2 pls] © The Palaeontological Association

TEXT-FIG. 1. The chambers of *Troglotella* (arrow) have grown into the alveoli of *Lithocodium*. A, thin section 86/28.2.10; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; ×23. B, drawing of the same specimen; scale bar represents 1 mm.



TEXT-FIG. 2. *Troglotella* occupying a chamber of *Lithocodium*. The connections between the chambers of *Troglotella* are partially visible. A, thin section COT IV 15 a; Cabeça beds, late Kimmeridgian; Cotovio near Albufeira, eastern Algarve, Portugal; ×37. B, drawing of the same specimen; scale bar represents 1 mm.

reefal crusts, where it occurs together with *Bacinella*, *Thaumatoporella* and calcareous microbial crusts. This life-style is known from several other foraminifers from other time periods, especially '*Bdelloidina*' *urgonensis* (Wernli and Schulte 1993) and acervulinid foraminifers (see Moussavian and Höfling 1993; Perrin 1994). *Lithocodium*, like some other microencrusters, is nearly always found autochthonous and is of great palaeoecological value (Leinfelder *et al.* 1993), indicating a shallow marine, reefal to lagoonal environment with normal salinity and moderate to elevated water energy. Thus, *Lithocodium* has proven to be a useful environmental indicator in areas where bathymetry is controversial, e.g. the Upper Jurassic of the Swabian Alb (Pl. 1, fig. 4; Leinfelder *et al.* 1994).

MATERIAL

Lithocodium, like most other microproblematica, has been known to date only from thin sections. The material presented here is of Late Jurassic age and consists of numerous thin sections, but also

includes a few three-dimensionally preserved specimens. The latter, as well as etched specimens, were examined under the SEM. Most samples are from Portugal (Lusitanian and Algarve Basins); others are from Spain (Celtiberian Basin), Southern Germany (Swabian Alb) and the Czech Republic (Stramberk). Stratigraphically, the samples range from the Oxfordian to the Tithonian. All specimens are in the collection of the Institut für Geologie und Paläontologie, University of Stuttgart.

In the following, locality and stratigraphical details are given for the illustrated material. Further information is in Leinfelder (1986, 1994*a*), Nose (1995), and Schmid and Jonischkeit (1995).

1. Middle Portugal, Lusitanian Basin:

1a. Ota Limestone (reef zone), 'middle' to upper Kimmeridgian: Alenquer (10 km north of Vila Franca de Xira), town quarry. Ota (15 km north of Vila Franca de Xira), valley south of Rio Ota.

1b. Amaral Formation, upper Kimmeridgian: Abadia near Montejunto (12 km north-west of Arruda dos Vinhos), 2·5 km south of the village. Amaral ridge (4·5 km north-east of Arruda dos Vinhos), south-eastern slope. Mata (1·5 km south-west of Arruda dos Vinhos), mountain ridge east of the village. Moinho da Chã (4 km north-west of Arruda dos Vinhos), 0·5 km south-east of the village.

1c. 'Pteroceriano' Formation, lower Tithonian: São Tiago dos Velhos (5 km south-west of Arruda dos Vinhos), 1·2 km south of the village.

2. Southern Portugal, Algarve Basin: Cotovio (3 km north-east of Albufeira), 2 km north of National Street N 125; Cabeça beds, upper Kimmeridgian. São Romão (7 km east of Loulé), 1 km north of the village; São Romão Limestone, lower Kimmeridgian.

3. Southern Germany, Swabian Alb: Wittlingen (4 km south-east of Bad Urach), 'Mockenrain' 1·5 km north-west of the village; coral limestones, lower Tithonian.

SYSTEMATIC PALAEONTOLOGY

In the following we will show that *Lithocodium* is a member of the Cyclamminidae which, according to Loeblich and Tappan (1988), is a group of loftusiid foraminifers. Genera now assigned to the Cyclamminidae or to the Spirocyclinidae were formerly classified as Lituolidae (see Loeblich and Tappan 1964) and therefore were known as lituolid foraminifers. They are now assigned to the Order Lituolida by Loeblich and Tappan (1992).

Class FORAMINIFERA Lee, 1990
Order LITUOLIDA Lankaster, 1885
Superfamily LOFTUSIACEA Brady, 1884
Family CYCLAMMINIDAE Marie, 1941
Subfamily CHOFFATELLINAE Maync, 1958

Genus LITHOCODIUM Elliott, 1956

Diagnosis. As the genus is regarded here as monospecific, its diagnosis is identical to that of the species.

Lithocodium aggregatum Elliott, 1956

Plate 1, figures 1–4; Plate 2, figures 1–6; Text-figures 1–8

1956 *Lithocodium aggregatum* Elliott, p. 331, pl. 1, figs 2, 4 [paratypes], 5 [holotype].
1959 'Problematikum A' Ohlen, p. 73, pl. 10, fig. 1; pl. 17, fig. 3 [quoted from Senowbari-Daryan 1980*b*].
1961 *Lithocodium japonicum* Endo, p. 64, pl. 5, figs 1–3; pl. 15, fig. 2.

1961 *Lithocodium morikawai* Endo, p. 64, pl. 12, figs 1–4; pl. 13, figs 3–4.
non 1964 'Problematikum 3' Flügel, p. 81, pl. 9, figs 1–2, 4 [in pl. 9 termed 'Problematikum 2' by mistake].
1968*a* *Lithocodium* cf. *L. aggregatum* Elliott; Johnson, p. 44, pl. 10, fig. 4.
non 1968*b* *Lithocodium regularis* Johnson, p. 13, pl. 2, fig. 3; pl. 4, figs 6–7.
1969 'Kavernöse Algenkrusten (Problematicum A, Ohlen)'; Zankl, p. 40, text-fig. 41.
1970 '*Lithocodium* Elliott and *Bouenia* [correct name: *Boueina*] Toula'; Bolliger and Burri, p. 38, pl. 9, fig. 2; pl. 11, fig. 1.
1970 *Belzungia* Morellet sp.; Golonka, p. 91, text-fig. 18.
1971 *Lithocodium* Elliott; Barthel *et al.*, p. 13, text-figs 7F, 8A.
non 1971 '*Lithocodium*-artiges Algen-Aggregat'; Barthel *et al.*, p. 15, text-fig. 8D.
non 1971 *Lithocodium aggregatum* Elliott; Basson and Edgell, p. 416, pl. 1, fig. 1.
non 1971 *Lithocodium regulare* Johnson [specific name corrected]; Basson and Edgell, p. 417, pl. 1, figs 2–3.
1971 *Lithocodium aggregatum* Elliott; Ramalho, p. 174, pl. 9. fig. 1; pl. 28, figs 3–5; pl. 29, fig. 1.
1972 *Lithocodium* Elliott/*Bacinella* Radoicic; Segonzac and Marin, pl. 11, figs 1–8.
1979 *Pseudolithocodium carpaticum* Misik, p. 709, pl. 2, figs 2–8.
1981 *Bacinella crispa* Eliasova, p. 30, pl. 2, fig. 3 [*partim*].
1984 *Bacinella morikawai* (Endo); Elias and Eliasova, pl. 1, fig. 4.
1985 *Bacinellacodium calcareus* Dragastan, p. 126, pl. 27, figs 1–3 [each *partim*].
v. 1986 *Lithocodium* Elliott sp.; Leinfelder, p. 60, pl. 12, figs 1–3.
1990 *Lithocodium aggregatum* Elliott; Banner *et al.*, p. 26, pl. 1, ?fig. 1, figs 2–4; ?pl. 2; pl. 3, fig. 1, ?figs 2–4; *non* pl. 4; *non* pl. 5; text-fig. 1. [The authors regard *Lithocodium* and *Bacinella* as synonyms.]
non 1992 *Lithocodium aggregatum* Elliott; Neuweiler and Reitner, pp. 274, 277, pl. 1; pl. 2, figs 1–2; pl. 3, figs 1–6. [The authors regard *Lithocodium* and *Bacinella* as synonyms.]
v. 1993 *Lithocodium* Elliott sp.; Leinfelder *et al.*, p. 202, pl. 42, figs 1–7; text-figs 6–7.
v. 1994*a* *Lithocodium* Elliott sp.; Leinfelder, p. 19, text-fig. 22.

Diagnosis (*emended*). Test multilocular, attached, chambers dome-shaped and roughly planispirally coiled or irregularly arranged in one or more layers; wall microgranular, calcareous and therefore probably a variable mixture of finely agglutinated and secreted calcite, may contain silt- to fine-sand-sized siliciclastic particles; wall dark in transmitted light, with imperforate thin outer layer (epiderm) and thick inner alveolar layer, forming a hypodermal meshwork; alveoli cylindrical, may bi- or trifurcate; attachment surface serving as a basal wall, substrate may be etched; aperture areal and cribrate; occasionally very thin dark lines crossing the chambers of the alveoli can be found, which appear to be phrenotheca-like structures; test commonly exhibiting a brownish coloration in reflected light, rarely white in very pure limestone.

Upper Jurassic specimens are commonly associated with a coelobitic foraminifer, *Troglotella incrustans* Wernli and Fookes (see below), appearing as bubble-like, often irregular structures within the chambers of *Lithocodium*. Outer diameter of chambers 0·8–3 mm; inner diameter of chambers 0·5–2 mm; wall thickness 0·5 mm; thickness of imperforate outer wall layer 8 μm; diameter of cylindrical alveoli 25–90 μm.

Remarks. The original description of Elliott (1956) is still regarded as being valid and is only enlarged and modified terminologically here, since Elliott interpreted *Lithocodium* as a codiacean alga. No significant differences exist between the Jurassic and the Cretaceous specimens described by Elliott, which can be verified best by examination of the paratype figured in his pl. 1, fig. 2.

The bubble-like structures mentioned in the diagnosis, actually representing a coelobitic foraminifer (see below), have been earlier interpreted as sporangia (Endo 1961). The species which have been defined mainly on account of this feature (*L. japonicum* and *L. morikawai*) must therefore be regarded as invalid.

Stratigraphical distribution. Anisian to Cenomanian, ?Turonian. According to Moussavian (1992), the taxon occurs up to the Campanian/?Maastrichtian; but the low magnification of the figures does not allow exact verification.

Superfamily HORMOSINACEA Haeckel, 1894
Family TELAMMINIDAE Loeblich and Tappan, 1985

Diagnosis. 'Test attached in the early stage only or throughout growth, consisting of a series of chambers that may be closely appressed or connected by stolonlike tubes; wall agglutinated; no obvious aperture other than the ends of the stolons' (Loeblich and Tappan 1988, p. 56).

Genus TROGLOTELLA Wernli and Fookes, 1992

Diagnosis. As the genus is monospecific, its diagnosis is identical to that of the species.

Troglotella incrustans Wernli and Fookes, 1992

Plate 1, figures 1–4; Plate 2, figures 1–6; Text-figures 1–8

1961	'Sporangia' (within *Lithocodium japonicum*); Endo, p. 64, pl. 5, figs 2–3; pl. 15, fig. 2.
1971	Unnamed structure (within *Lithocodium*); Barthel *et al.*, text-figs 7F, 8A.
1971	Unnamed structure (within *Lithocodium*); Ramalho, pl. 9, fig. 1; pl. 28, figs 3–5; pl. 29, fig. 1.
1981	*Bacinella crispa* Eliasova (within *Lithocodium*), p. 30, pl. 2, fig. 3.
1985	*Micrisphaera ovalis* [author = ?] (sporangia within *Lithocodium*); Connally and Scott, text-fig. 9D.
1985	*Bacinella* Radoicic (within *Lithocodium*); Hüssner, pl. 17, fig. 7.
v. 1986	'Sporangia' (within *Lithocodium*); Leinfelder, p. 60, pl. 12, figs 1–2.
1986	'Mikroproblematikum 10' Werner, pl. 16, figs 8–10.
v. 1989	*Bullopora* aff. *laevis* Sollas; Leinfelder, pp. 51, 56, pl. 2, fig. 6; pl. 3, fig. 5; pl. 4, fig. 5.
1991	Unnamed structure (within *Lithocodium*); Darga and Schlagintweit, pl. 2, fig. 6.
1992	'Structures globuleuses'; Bodeur, pl. 18, figs 1–2 [*partim*], 3–4, 11.
1992	*Troglotella incrustans* Wernli and Fookes, p. 97, pls 1–2.
v. 1993	*Bullopora* aff. *laevis* Sollas; Leinfelder *et al.*, p. 203, pl. 40, fig. 2; pl. 42, figs 2–7.
v. 1994*a*	?*Bullopora* aff. *laevis* Sollas; Leinfelder, pp. 19, 24, text-figs 22, 25.

Diagnosis (*emended*). The test of *Troglotella incrustans* exhibits two different stages. The juvenile stage is uniserial, slightly curved, consisting of not more than seven or eight chambers and may be situated in a cavity bored by the foraminifer itself, whereas the adult stage encrusted the surface of the substrate. In most cases, *Troglotella incrustans* dwelt in the chambers of the foraminifer *Lithocodium aggregatum* Elliott, 1956, often without boring activity in the juvenile stage. Chamber form in the juvenile stage is spherical to cylindrical, in the adult stage it is commonly irregular or pyriform. Juvenile chambers closely adjacent, later chambers may be separated by stolon-like necks; aperture single, terminal, at the open end of the stoloniferous necks. Wall thin, microgranular, calcareous, imperforate, probably agglutinated; dark in transmitted light. According to the original authors (Wernli and Fookes 1992), short and stocky forms are thought to represent the megalospheric generation, whereas long and slim forms would represent the microspheric generation. The measurements taken from our material are as follows: total length up to 2 mm; diameter of proloculus 50–70 μm (presumed 'microspheric' form); maximum diameter of regular chambers (juvenile stage) 250 μm; maximum diameter of irregular, tube-like chambers 1 mm; number of chambers in juvenile stage not more than seven or eight; length of juvenile part of the test 600–700 μm; total number of chambers 12 to 15; wall thickness 5–10 μm.

Remarks. Our diagnosis contrasts partly with the observations of Wernli and Fookes (1992), who state that the juvenile stage may reach 1·9 mm in length, visible in one specimen (Wernli and Fookes 1992, pl. 1, figs 1, 4). In our opinion, only the first seven to eight chambers, with a maximum length of 700 μm, represent the juvenile stage, characterized by the regular, spherical to cylindrical

chamber form (Pl. 1, fig. 1; Text-fig. 6). Later chambers are mostly irregular, but may rarely retain a regular shape. The adult stage of the specimen figured in Wernli and Fookes (1992, pl. 1, fig. 2) is thought to reach 4 mm in diameter, which is not verifiable from the figure itself. Wernli and Fookes (1992) suggested the existence of both microspheric and megalospheric forms. This is plausible and substantiated by their figures. However, due to the irregular morphology of the test and the impossibility of isolating it from the hard calcareous host rocks, thin section material may show all ranges from a very small to a fairly large first chamber. It must be assumed that the proloculus is not always cross-cut at its largest diameter, due to the irregularity of the test, which makes identification of microspheric and megalospheric forms difficult.

Probably, *Troglotella incrustans* was able to branch, although the evidence provided by the present thin section material is equivocal. Branching foraminifers are known particularly among the Telamminidae (see Loeblich and Tappan 1988), but do also occur within several other groups.

Attribution to the Lituolida. The imperforate, microgranular fabric of the wall (pl. 2, fig. 6), which is dark in transmitted light, occurs similarly in miliolids. In reflected light, however, the brownish colour of the test contrasts with the typical bright white coloration of the miliolids, and clearly excludes an attribution to this group. Wernli and Fookes (1992) tentatively attributed the taxon, with some reservations, to the Telamminidae. The features detected in the present material substantiate this interpretation.

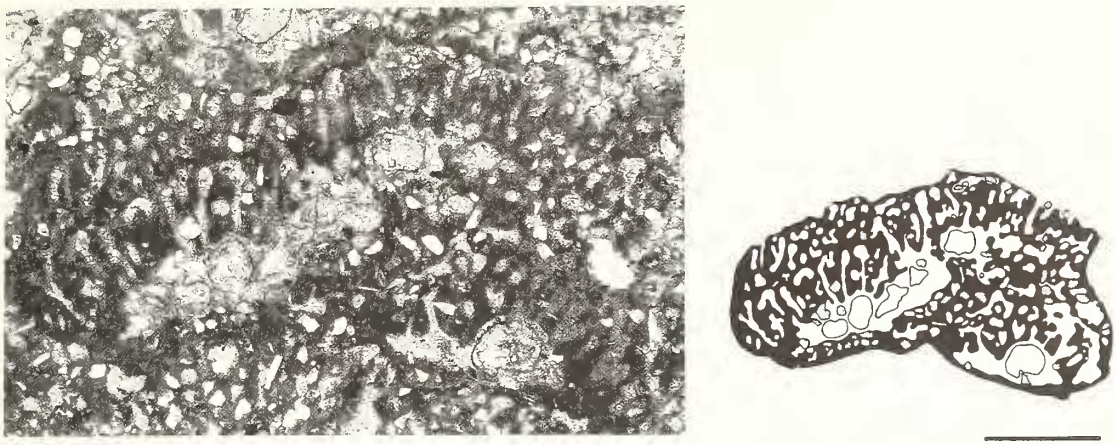
Life habit and association. Troglotella incrustans was a facultative borer in its juvenile stage, boring perpendicularly into its substrate (Pl. 2, fig. 5, Text-fig. 6). Wernli and Fookes (1992), despite clearly figuring boring specimens, alternatively suggested cryptic settlement within pre-existing cavities or borings of other, unknown, organisms (for discussion see below). Other specimens do not exhibit an early boring stage but only inhabited pre-existing cavities. Later growth stages expanded over the substrate, either in an epibenthic fashion or, much more commonly, within pre-existing cavities. In our material, the vast majority of *Troglotella* grew within the chambers of *Lithocodium aggregatum* (Superfamily Loftusiacea), in very shallow, generally wave-agitated settings.

Stratigraphical distribution. Oxfordian to Tithonian.

DETAILED DESCRIPTION OF *LITHOCODIUM* AND DISCUSSION

Wall characteristics

The wall of *Lithocodium* is microgranular, i.e. dense, dark, and therefore probably originally calcitic (Pl. 2, fig. 6). In reflected light, *Lithocodium* shows a brownish to reddish coloration in most samples, which is a typical feature of agglutinating foraminifers (Haynes 1981). Consequently, the microgranular wall structure can be interpreted as finely agglutinated, a feature typical of loftusiid as well as orbitolinid foraminifers and others. Some authors (e.g. Podobina 1990) consider microgranular walls as being secreted in a similar manner to those of the fusulinids. In any case, *Lithocodium* was able to agglutinate detrital particles, which is particularly evident when siliciclastic material is incorporated (Text-fig. 3). Within the loftusiid foraminifers, all transitions from walls composed solely of coarsely agglutinated particles (e.g. *Flabellamminopsis*) to walls with a purely microgranular structure (e.g. *Alveosepta jaccardi*) exist. The tests of *Rectocyclammina* or *Otaina magna*, for example, are composed of both coarse, agglutinated and microgranular material. The amount of coarse particles appears variable (cf. Ramalho 1990), a feature which is consistent with the observations on *Lithocodium*. In *Lithocodium*, incorporation of considerable amounts of silt- to fine-sand-sized siliciclastics (quartz, feldspar, mica; Text-fig. 3) occurs only in terrigeneously contaminated settings; this is similar to the situation in other loftusiid taxa such as *Rectocyclammina*. Despite its rarity, explicable by the strong preference of *Lithocodium* for pure carbonate settings, this is a strong additional argument against the codiacean affinities of *Lithocodium*.



TEXT-FIG. 3. *Lithocodium* nodule containing a high percentage of detrital quartz. The chambers are occupied by *Troglotella*. A, thin section Ab I 7; Amaral Formation, late Kimmeridgian; Abadia near Montejunto, Lusitanian Basin, Portugal; ×26. B, drawing of the same specimen (siliciclastic particles are stippled); scale bar represents 1 mm.

The numerous alveoli in the wall are responsible for the complex labyrinthic wall fabric, a feature typical for all loftusiid and orbitolinid foraminifers. Alveoli of *Lithocodium* can be bi- or trifurcate (Ramalho 1971, p. 174; Text-fig. 1), which makes them appear like algal filaments or cyanobacterial trichomes. However, well preserved material often shows that the alveoli are coated by an outer imperforate layer. The outer layer prevents penetration of sediment even into dead tests, which explains why all cavities are preserved by calcitic spar, unless the test was damaged. Alveoli covered by a thin wall clearly exclude an algal origin but are a typical feature of all loftusiid foraminifers, which are imperforate. In well preserved specimens, where preservational bias can be ruled out, open, spar-filled alveoli are interpreted as representing openings to the adjacent chamber. The generally imperforate nature of *Lithocodium*, as well as the dense, hence probably originally calcitic, structure of its wall has already been noticed by Persoz and Remane (1973, p. 59, pl. 2, fig. 3) who therefore doubted its codiacean nature, without, however, suggesting other explanations.

Thin section analysis reveals that these chamber openings of *Lithocodium* are cribrate. The same is assumed for *Paracyclammina* whose openings are also known only from thin sections (Loeblich and Tappan 1988, p. 102).

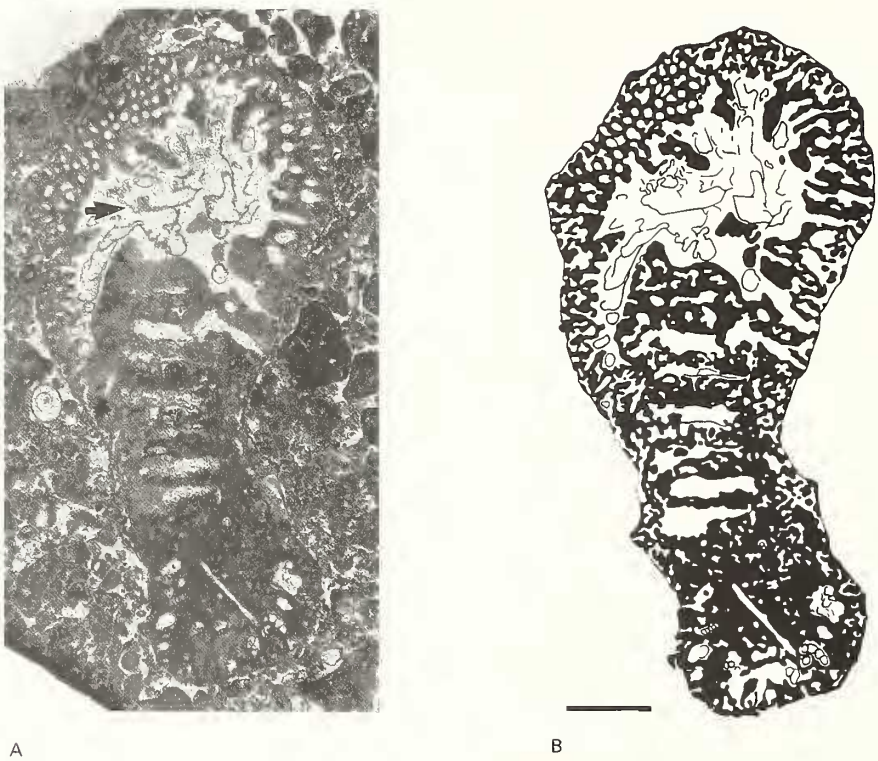
General growth form and comparison with other loftusiid taxa

An attribution of *Lithocodium* to the Cyclamminidae is not only evident by the labyrinthic, originally calcitic, wall structure but, partly, also by the dimensions and hemispherical shape of the chambers of *Lithocodium*.

Paracyclammina (Loeblich and Tappan 1988, pl. 99, figs 10–13), *Pseudocyclammina* (Loeblich and Tappan 1988, pl. 102, figs 4–6) or *Loftusia* (Loeblich and Tappan 1988, pl. 116, fig. 10) exhibit wall structures virtually identical to those of *Lithocodium*, but differ in dimensions and general growth form. Some cross sections do not allow differentiation between *Lithocodium* and other loftusiid foraminifers. Close similarity exists with *Pseudocyclammina lituus* (cf. Maync 1959, pls 1–6; Hottinger 1967, text-fig. 29*a–b*, pl. 10, figs 11–13), which is particularly similar to *Lithocodium* not only in respect of its wall characteristics, but also regarding its general growth form, although it

exhibits smaller chambers. *Pseudocyclammina* tests, though often planispiral, may instead exhibit a streptospiral juvenile growth stage and may become uncoiled in the adult stage (Loeblich and Tappan 1988). Chamber dimensions and the uncoiled adult growth stage of *Rectocyclammina* are also comparable with *Lithocodium*, although the alveolar fabric of the wall differs (Ramalho 1971, pl. 14, fig. 2). This is also true for *Otaina magna*, which may look quite similar to *Lithocodium* in some sections (Pl. 1, fig. 6) but differs from the latter by incorporating coarse bioclasts in its wall (cf. Ramalho 1990). *Loftusia farsensis*, of Maastrichtian age, is almost identical with *Lithocodium* in the structure of its alveolar wall and distinct hemispherical shape of its chambers, and the relation between wall and chamber dimensions (cf. Mehrnusch 1985, text-fig. 2, figs 1–2), but differs from the latter by the smaller dimension of the chambers and by its planispiral growth.

Leinfelder (1989, pl. 4, fig. 5; 1994*a*, text-fig. 2) figured a large, coiled 'lituolid' foraminifer and mentioned close similarities with *Lithocodium* both in the structure of the wall and in the existence of the coelobitic foraminifer '*Bullopora* aff. *laevis*' (identical to *Troglotella incrustans*). Re-examination shows that no differences from *Lithocodium* exist so that the foraminifer is interpreted now as a planispirally coiled specimen of *Lithocodium* (Text-fig. 4). In other thin sections, both the



TEXT-FIG. 4. Coiled specimen of *Lithocodium*. The chambers are occupied by *Troglotella* (arrow), whose test walls are not completely preserved. A, thin section SOT 1; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; × 12. B, drawing of the same specimen; scale bar represents 1 mm.

diameter and the alveolar size of subsequent small *Lithocodium* chambers may increase in a regular fashion, which also might indicate a coiled juvenile growth stage (Pl. 2, fig. 2). Moreover, *Lithocodium* specimens in three dimensional preservation show a more or less well developed coiled

chamber arrangement (Text-fig. 5). All these features are also shown in the model of *Lithocodium* (Text-fig. 7), reconstructed from numerous thin sections.

A difference from *Pseudocyclammina* or *Rectocyclammina* is the dominantly encrusting growth of *Lithocodium* during later growth stages. Irregular growth along the substrate is known from *Anchispirocyclina lusitanica*, another large Upper Jurassic/Lower Cretaceous loftusiid foraminifer, which may also bifurcate (cf. Ramalho 1971, p. 148, pl. 15, figs 6–7; pl. 16).

According to Septfontaine's (1980) determination key for imperforate Mesozoic foraminifers, *Lithocodium* falls in 'group C2' (planispirally coiled, later uncoiled and rectilinear, with subepidermal layer without pillars, aperture multiple, test attached) and hence is a close relative of *Pseudocyclammina*, which only differs from the latter in its more irregular growth and larger chambers.

Occasionally, the calcareous substrate of *Lithocodium* shows etching and dissolution features, e.g. thin bivalve shells which are partly dissolved in places where overgrown by *Lithocodium* (Pl. 2, fig. 3). This indicates that *Lithocodium* normally had no basal wall, although in some cases a minute dark basal layer is visible. This is another argument against an interpretation of it as an encrusting alga which normally are attached by a basal skeleton. Sessile foraminifers rarely produce a basal wall below their chambers, since normally (i.e. in coiled forms) the outer walls of preceding chambers serve as substrate. It is known from other encrusting foraminifers, such as the Cretaceous '*Bdelloidina*' *urgonensis* (Wernli and Schulte 1993, pl. 1, figs 5, 8) or the Palaeozoic form *Oxinoxis* (Loeblich and Tappan 1988, p. 64), that the attachment surface may serve as basal wall.

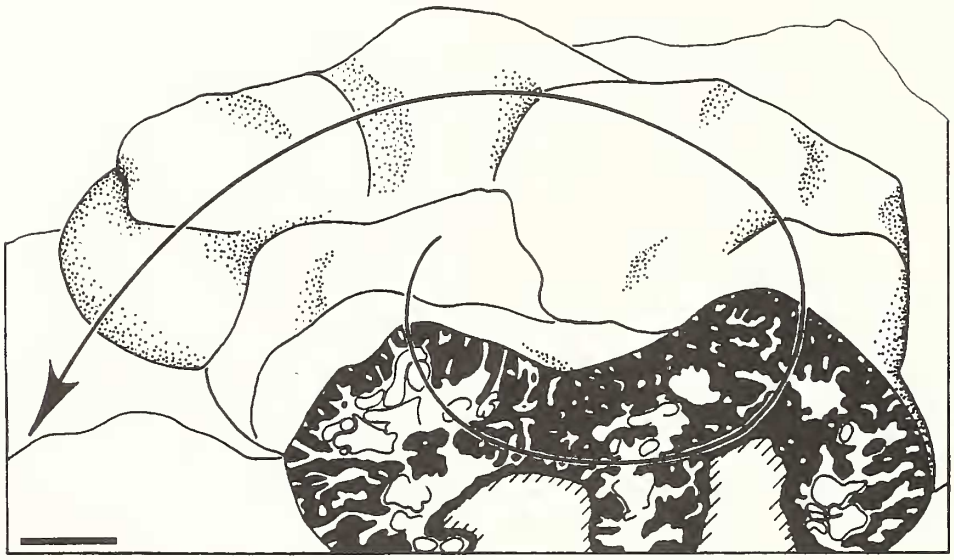
Association with other encrusting organisms

The chambers of Upper Jurassic *Lithocodium* are very commonly occupied by the coelobitic foraminifer *Troglotella incrustans* (see below). *Troglotella incrustans* may also occur outside *Lithocodium*, but never within the test of other foraminifers. *Lithocodium* is furthermore commonly associated with the micro-encrusters *Bacinella* and *Thaumatoporella*, both of which are of uncertain, probably cyanobacterial and algal affinity, respectively. Cayeuxiid cyanobacteria and solenoporacean red algae may co-occur as well. *Lithocodium* is typical of reefal, coral-rich settings as well as non-reefal oncoid environments.

Invalidity of other Lithocodium *species and of the genera* Bacinellacodium *and* Pseudolithocodium

The synonymy list of *Lithocodium aggregatum* presented above shows that we consider all species other than the type species, *L. aggregatum*, as invalid. This is based on the fact that the bubble-like structures present in the chambers of some specimens of *L. aggregatum* (e.g. Pl. 1, fig. 4; Text-figs 3, 7) clearly represent a coelobitic foraminifer (see below) and not calcified sporangia of *Lithocodium*. The latter was assumed by Endo (1961) who separated species with such 'sporangia' from the sporangia-lacking *L. aggregatum*. He established the 'sporangia'-bearing species *L. japonicum* and *L. morikawai* on the basis of the tertiary branching of the filaments (now alveoli) of *L. morikawai*. The present rich material shows that filaments of all sizes and kinds in the range of the above specimens may exist even within one large *Lithocodium* specimen (e.g. Pl. 1, figs 2–3). Differences are due both to variations between juvenile and adult growth stages, and to artificial effects of two-dimensional sampling. All criteria given and figured for the taxa *Pseudolithocodium carpaticum* and *Bacinellacodium calcareus* also fall in the variability of our *Lithocodium aggregatum* material. Consequently, all recorded species of *Lithocodium*, as well as the last two genera, are presumably invalid, although this conclusion is not based on the examination of the original material. *Lithocodium regulare* Johnson is not identical to *Lithocodium aggregatum*, but probably to *Pseudocyclammina* (see below).

A



B

TEXT-FIG. 5. Three-dimensionally preserved specimen of *Lithocodium*; the chambers are occupied by *Troglotella* (arrow). A, CHA 1/F, scanning electron micrograph; Amaral Formation, late Kimmeridgian; Moinho da Chã near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×12. B, drawing of the same specimen. The arrow indicates the spiral succession of the *Lithocodium* chambers; scale bar represents 1 mm.

EARLIER INTERPRETATIONS OF *LITHOCODIUM*

Codiacean nature?

Earlier authors attributed *Lithocodium*, partly with reservations, to the codiacean green algae (e.g. Elliott 1956; Ramalho 1971; Jaffrezo 1974). The following features described above argue against this: (1) dark in transmitted light due to the presumed original calcitic fabric; fossil codiaceans, such as *Boueina*, are always light under transmitted light due to the recrystallized character of the original aragonite skeleton; (2) ability to agglutinate siliciclastic particles; (3) encrusting life-style; and (4) clearly to crudely coiled during early growth stages.

A single Lithocodium-Bacinella *organism?*

Parts of structures described as *Bacinella* are identical to *L. aggregatum* (see synonymy list). This confusion is partly a result of considering *Bacinella* (Pl. 1, fig. 5) as the older, valid name for the same organism described as *Lithocodium*. Actually, *Lithocodium* and *Bacinella* are often intimately associated and may commonly overgrow each other. This led to the assumption that the two taxa are parts of one single organism, either representing cortex and medulla, respectively, of a codiacean alga (Banner *et al.* 1990), an organism *incertae sedis* (Segonzac and Marin 1972), or different ecological varieties of an enigmatic organism (Maurin *et al.* 1985; Neuweiler and Reitner 1992). If it is true that *Bacinella* is a microbe (Maurin *et al.* 1985), possibly a cyanobacterium (Schäfer and Senowbari-Daryan 1983), this would imply that *Lithocodium* also represents a different ecological variety of the same cyanobacterium. Agglutination of detrital material, as observed in the present material, would be compatible with a cyanobacterian character. However, the regular growth form and, particularly, the outer imperforate layer clearly exclude a cyanobacterian nature for *Lithocodium*. It should be mentioned that Schäfer and Senowbari-Daryan (1983), though considering *Bacinella* to be a cyanobacterian microbe, did not see any relation to *Lithocodium* which was interpreted as a codiacean alga. Generally, the interpretation of genomic identity of *Bacinella* and *Lithocodium* is not followed by most authors or is clearly rejected (e.g. Conrad 1969, p. 63; Wnendt-Juber 1990, p. 101; Leinfelder *et al.* 1993), based on the fact that both taxa may occur together in the same environment, without overgrowing each other, or simply occur without each other.

Confusion with *Bacinella* has resulted particularly from the occasional occurrence of phrenotheca-like structures which may cross chambers or even alveoli of *Lithocodium* in various places and at various angles (Pl. 2, fig. 1; Text-figs 7–8). They are irregular, thin, dense partitions which may be interconnected and hence appear in a mesh-like, 'bacinellimorph' fashion. Phrenotheca are facultative structures of unknown function which occur in some fusulinids, particularly in *Pseudofusulina* (Loeblich and Tappan 1964, fig. 291; 1988, pl. 283, fig. 8). Similar structures also occur in some loftusiid foraminifers, such as *Valvulina lugeoni* (Septfontaine 1980, pl. 3, fig. 7) as well as in other foraminiferal groups (e.g. *Biokovina*, cf. Loeblich and Tappan 1988, pl. 82, figs 2–4). We also detected them in Portuguese material of *Otaina magna*, although they are not mentioned in the original description by Ramalho (1990, pl. 2, fig. 1; pl. 3, fig. 1).

Phrenotheca-like, 'bacinellimorph' structures are common in Triassic and Cretaceous *Lithocodium* but also occur occasionally in Upper Jurassic material (see below). Confusion of phrenotheca-like foraminiferal structures with *Bacinella irregularis*, an enigmatic organism of unclear systematic position, can be avoided when restricting *Bacinella* to clearly epibenthic meshwork crusts of noticeable thickness and extension.

Attribution to multicellular animals?

Leinfelder (1986) assigned *Lithocodium* to the '*incertae sedis*'. However, he noticed certain similarities to multicellular animals in the complex character of the labyrinthic wall, the detection of occasional cross-partitions within 'filaments' (i.e. alveoli), and the existence of larger cavities.

Hydrozoans and stromatoporoids show similarities in the occurrence of both horizontal and vertical elements. However, the present material shows that cross-partitions are a rare, possibly secondary, feature and the basal cavities of *Lithocodium* cannot represent an astrorhizal system of stromatoporoids but rather are individualized chambers. The character of stacked chambers, as well as the multiporous connections between them, show some similarities with segmented coralline sponges (sphinctozoans). General size, labyrinthic wall structure, the partly coiled nature and the ability to agglutinate detrital particles clearly stands against such an interpretation, although it should be noticed that general morphological similarities between foraminifers and sphinctozoans may exist. An example is the Triassic problematical form *Cheilosporites tirolensis* Wähner which was interpreted as foraminifer by Fischer (1962) and as sphinctozoan sponge with microcrystalline wall structure by Senowbari-Daryan (1980*a*).

Earlier 'near misses' of the foraminiferan character

Interestingly, some earlier interpretations already approached the idea of the foraminiferan character of *Lithocodium*, but the authors failed to recognize it.

Senowbari-Daryan (1980*b*), after a similar suggestion by Schäfer (1979), identified 'Problematicum A' Ohlen (1959) as a younger synonym of *Lithocodium aggregatum*. Some confusion was caused by another similar enigmatic encruster, which had been described by Flügel (1964, p. 81; 1972, p. 966) as 'Problematicum 3'. Flügel interpreted this coarse agglutinating organism as a foraminifer and compared it with 'Problematicum A' Ohlen (i.e. with *Lithocodium* according to Senowbari-Daryan 1980*b*). Zankl (1969, p. 46, text-fig. 57) described the same form, 'Problematicum 3' Flügel (1964) also as a sessile foraminifer. However, Senowbari-Daryan (1980*b*, p. 90) rejected the synonymy of 'Problematicum 3' Flügel with 'Problematicum A' Ohlen/*Lithocodium* but rather noticed similarities of 'Problematicum 3' to the loftusiid foraminifer *Labyrinthina* Weynschenk.

Schäfer (1979) noted that 'Problematicum A' Ohlen/*Lithocodium* could be placed either within the codiaceans or within the foraminifers, but this interpretation is obviously based on the erroneous synonymization of 'Problematicum 3' Flügel and 'Problematicum A' Ohlen (see above).

Johnson (1968*b*) established the species *Lithocodium regularis* (later corrected to *L. regulare* by Basson and Edgell 1971). Originally assuming a codiacean character, Johnson later noticed the foraminiferan character of the form (Johnson 1969, p. 38). In our opinion, it probably represents the genus *Pseudocyclammina*, as the chamber dimensions are too small for *Lithocodium*.

EXPLANATION OF PLATE 1

Fig. 1. *Lithocodium* chamber, occupied by *Troglotella* and overgrown by the stromatoporoid *Burgundia trinorchii*. Acetate peel M I 6; Amaral Formation, late Kimmeridgian; Mata near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×23.

Figs 2–3. 2, Thick *Lithocodium* crust, overgrowing *Marinella lugeoni* (left). Spirally arranged chambers (arrow) indicate a coiled growth stage. All chambers are occupied by *Troglotella*. Thin section SV 26a; 'Pteroceriano' Formation, early Tithonian; São Tiago dos Velhos near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×8. 3, Detail of part of fig. 2 (from right hand side). Chamber formation is progressing from left to right, as shown in Text-fig. 8; ×18.

Fig. 4. *Lithocodium*, overgrowing and overgrown by *Pseudochaetetes polyporus* and an oyster. All chambers are occupied by *Troglotella*. Thin section WIT 1/1; coral limestones, early Tithonian; Wittlingen near Bad Urach, Swabian Alb, Germany; ×15.

Fig. 5. The meshwork structure of *Bacinella irregularis*, an enigmatic microencruster which is commonly, though not necessarily associated with *Lithocodium*. Thin section RO 112; São Romão Limestone, early Kimmeridgian; São Romão near Loulé, eastern Algarve, Portugal; ×12.

Fig. 6. *Otaina magna*, a loftusiid foraminifer with a structure similar to that of *Lithocodium*. Thin section 86/26.2.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; ×23.

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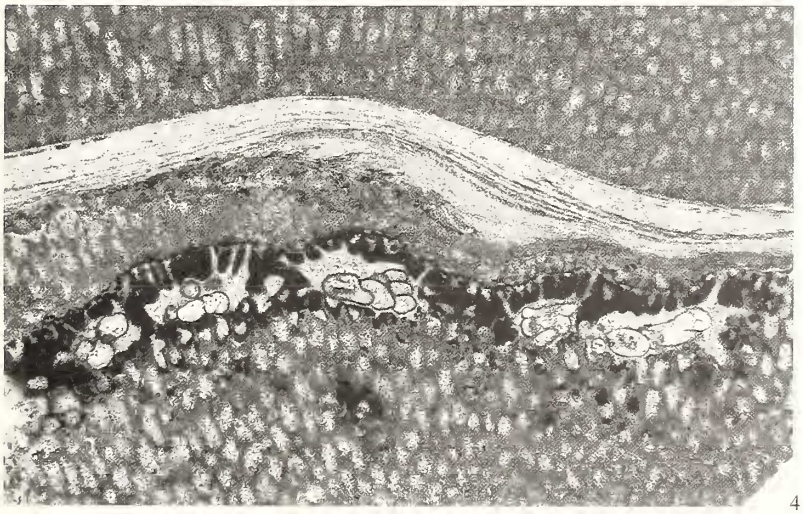

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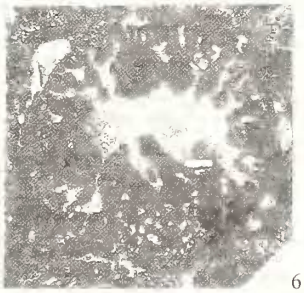

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SCHMID and LEINFELDER. *Lithocodium-Troglotella* foraminiferal consortium

Segonzac and Marin (1972) noticed some similarities to the foraminifer *Coscinophragma* but concluded that other features, particularly the presumed identity with *Bacinella* (see above), were not compatible with a foraminiferan character.

Leinfelder (1989, 1994*a*) described coiled 'lituolid' foraminifers with a close similarity to the *Lithocodium* structure, but did not synonymize both, due to the fact that the figured specimen represented the only known coiled exemplar at that time (see above).

ECOLOGICAL REQUIREMENTS AND LIFE STRATEGY OF *LITHOCODIUM*

Both the association with reefal and non-reefal microbial crusts, and typical shallow-water organisms such as corals, stromatoporoids, dasycladacean algae or red algae show that *Lithocodium* was a fully marine, shallow-water organism (Leinfelder *et al.* 1993). As an encruster, it demanded a low background sedimentation rate and commonly grew alternating with other organisms such as microbial or algal-type organisms (e.g. *Bacinella* or *Thaumatoporella*) or stromatoporoids (particularly *Burgundia*). *Lithocodium* frequently also contributed to the formation of oncoid cortices where it co-occurred with microbial crusts, *Bacinella*, cayeuxiid cyanobacteria, red algae, nubeculariid and placopsilinid foraminifers as well as bryozoans. Besides lagoonal low-energy settings, it more commonly occurred in debris-rich, high-energy reefs (Leinfelder 1992), indicating its tolerance of elevated water energy. Pure carbonate environments were preferred but a certain influx of siliciclastic material could be tolerated, whereby the siliciclastic particles may have become incorporated in the test (see above). Being readily identifiable, *L. aggregatum* is a valuable palaeoecological indicator.

L. aggregatum commonly occurs in colonies, i.e. various specimens or generations overgrew each other forming flat to domal, crustose colonies which are up to several tens of millimetres thick and broad (Pl. 1, figs 2–3). Pure *Lithocodium* nodules (Pl. 2, fig. 4) and oncoids exist as well. With the additional participation of *Bacinella* and microbial crusts they may attain diameters of up to 100 mm. To a small extent, *Lithocodium* may also have contributed to reef formation, partly acting as a binder but more as a constructor. This is a close analogue of the agglutinating Cretaceous foraminifer '*Bdelloidina*' *urgonensis* (cf. Schulte *et al.* 1993; Wernli and Schulte 1993) and of acervulinid foraminifers, including the formerly supposed red alga *Solenomeris*, from the Tertiary. *Solenomeris* was regarded as a foraminifer by only a few authors, such as Trauth (1918; see Hagn and Wellnhofer 1967), and was identified as a reef-building foraminifer by Perrin (1987; see also Plaziat and Perrin 1992). Moussavian and Höfling (1993) regarded *Solenomeris* as a synonym of *Acervulina*, a view which was rejected by Perrin (1994).

'*Bdelloidina*' and *Solenomeris* show very similar growth form and environmental distribution to *Lithocodium*, except that *Solenomeris* is able to build large biostromes and bioherms up to several metres thick. Recent acervulinid foraminifers such as *Acervulina* also contribute to the formation of oncoids or 'macroids', e.g. in the Red Sea and the Mediterranean Sea (Hottinger 1983). This special life strategy of forming bioconstructions is also known from the miliolid foraminifer *Nubecularia*, which forms, or contributes strongly to the formation of oncoids in the Middle Jurassic of the Paris Basin (e.g. Hilly and Haguenauer 1979) and Lusitanian Basin, Portugal (cf. Leinfelder 1983, pl. 1). Nubeculariid foraminifers are also able to build small bioherms (0·5 m), as known from the Middle Miocene of Bessarabia/Eastern Paratethys (Gillet and Derville 1931) and are also major constituents of the biostromes reported from the Middle Miocene of Austria/Central Paratethys (Friebe 1994). Recent counterparts of *Lithocodium* do not exist among the Lituolida; *Bdelloidina* is the only living larger foraminifer in this group (cf. Loeblich and Tappan 1988). The encrusting life style and the alveolar wall structure of this genus resemble those of *Lithocodium*, but the coarsely agglutinated wall and the apparent absence of algal symbionts represent important differences. The Recent rotaliid genus *Homotrema* is an encrusting foraminifer which very probably harbours algal symbionts (Strathearn 1986) and contributes to reef formation; therefore, it may be compared with *Lithocodium*.

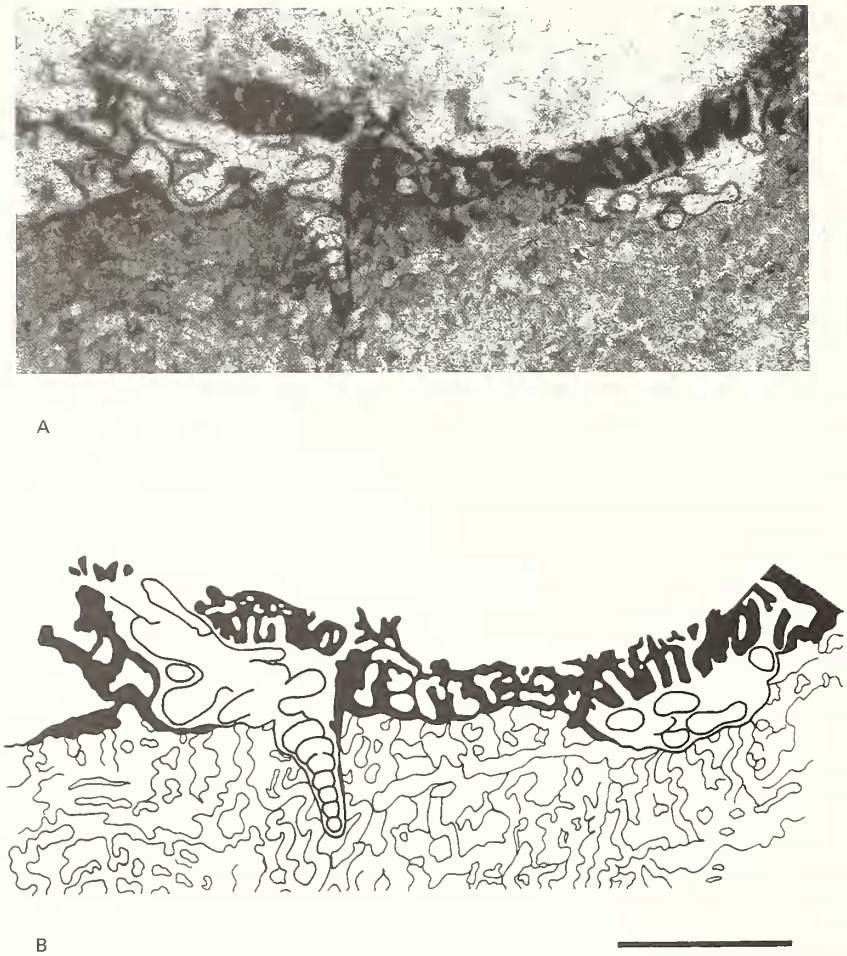
The suggestion seems plausible that the irregular, consistently flat growth form of *Lithocodium*, which spread across the substrate (Pl. 1, fig. 4), was an adaption to shallow marine environments in order to enlarge the surface area in order to receive more light for symbiotic algae (cf. Cowen 1983, p. 450; 1988, text-fig. 2). According to Hallock (1985, p. 205), 'algal symbiont-bearing organisms have tremendous energetic advantage over similar organisms lacking symbionts under nutrient-deficient conditions'. Generally, feeding plays only a minor role in larger symbiont-bearing foraminifers and merely supplies metabolites such as vitamins which are not synthesized within the association (Lee and Anderson 1991, p. 200). Symbiotic unicellular algae (diatoms, dinophyceans, rhodophyceans, chlorophyceans and chloroplasts) are common in miliolid and rotaliid foraminifers, especially in large forms (Röttger 1972; Haynes 1981; Lee and McEnery 1983; Leutenegger 1984; Lee and Anderson 1991; Murray 1991) and have also been recorded from one agglutinated species (Knight and Mantoura 1985, p. 245). Ross (1979, p. 59) stated that, besides the general flattened shape of larger foraminifers, complex wall structures appear also to be adaptations to a symbiotic relationship with algae. According to Leutenegger (1984, p. 33), most symbiont-bearing foraminifers possess pore cups or separated chamber compartments, which serve to stabilize the symbiont's preferred position directly below outer chamber walls, avoiding larger cytoplasmic currents which could carry the algae away. Additionally, Lee and McEnery (1983, p. 57) suggested that this feature could be a mechanism to segregate algal endosymbionts from the digestive vacuoles of the host.

In *Lithocodium*, as well as in other loftusiids, the alveoli in the test wall could be an adaptation to house symbiotic algae. The existence of symbionts in larger agglutinated foraminifers with complex wall structures was also suggested by Hottinger (1984, p. 313). The restriction of *Lithocodium* to shallow marine, mostly reefal (hence nutrient-depleted) environments, their irregular, flat morphology, and their large size, are good arguments for a symbiosis with unicellular algae (see 'check-list' in Cowen 1988, text-fig. 2). Most modern foraminifers with zooxanthellate symbionts show a relatively wide bathymetric distribution, whereas foraminifers with chlorophycean symbionts ('zoochlorellae') are restricted to very shallow water (Leutenegger 1984). The association of *Lithocodium* with distinct shallow-water faunal elements such as reef building corals is indicative of its shallow habitat (Leinfelder *et al.* 1993) and might therefore hint at a chlorophycean nature of the *Lithocodium* symbionts, although some modern zooxanthellate foraminifers (e.g. *Marginopora vertebralis*) are also restricted to very shallow settings (cf. Leutenegger 1984). However, a flat growth form in foraminifers is not an unequivocal indicator for algal symbiosis, since some extant species of larger, flat foraminifers are living without symbionts (see discussion in Cowen 1983, p. 454; Leutenegger 1984; Hallock 1985; Brasier 1986; Murray 1991).

Leutenegger and Hansen (1979) demonstrated that the pores of perforate foraminifers, although covered by a thick organic lining, serve for gas exchange. In non-symbiont bearing species, the pores serve the purpose of oxygen uptake, as indicated by the concentration of mitochondria below the pores, whereas in symbiont-bearing species CO_2 passes inward through the pores when the symbionts are active (Leutenegger and Hansen 1979, p. 15). Hansen and Dalberg (1979) showed that the thin walls of the pseudopores of some miliolid foraminifers permit the passage of CO_2 for use by symbiotic algae, as observed in living *Amphisorus*. They suggested an identical mechanism for other miliolid foraminifers with thin lateral walls. If this is true, the same can be assumed for *Lithocodium*, since its epidermal layer is similarly thin. In addition, Hottinger (1986, p. 226) suggested that the thin outer walls of lituolid and fusulinid foraminifers also probably served for the exchange of small molecules.

DETAILED DESCRIPTION OF *TROGLOTELLA* AND DISCUSSION

Lithocodium was thought to exhibit calcified sporangia (Endo 1961). Leinfelder (1989, p. 51, pl. 3, fig. 5; pl. 4, fig. 5; identical with Leinfelder 1994*a*, text-fig. 22) identified these bubble-like structures within *Lithocodium* cavities as cryptic foraminifers and provisionally attributed them to *Bullopora* aff. *laevis* and ?*Bullopora* aff. *laevis*. Further figuring and a brief description of this foraminifer was



TEXT-FIG. 6. *Troglotella* within *Lithocodium*, clearly boring into a microsolenid coral whose septa are cut. The shape of adult chambers is adapted to the inner surface of the *Lithocodium* chamber. The roof of this chamber was either partially eroded or lifted off by *Troglotella*. A, thin section 7/17.4.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; ×23. B, drawing of the same specimen; scale bar represents 1 mm.

later given by Leinfelder (1992) and Leinfelder *et al.* (1993, p. 203; text-figs 6–7; pl. 42, figs 1–7). This foraminifer has now been identified as *Troglotella incrustans* Wernli and Fookes, 1992.

Structure, morphology and function of the test

Lituolid foraminifers with microgranular walls of very minute agglutinated particles or with a dominance of calcitic matrix are common (cf. Hansen and Abd-Elshafy 1988). No pores are visible in thin section and under SEM examination (Pl. 2, fig. 6). Sometimes, poorly preserved specimens show diagenetic crystal enlargement which may result in a partly hyaline, pseudoporous structure. Although originally taken as characteristic for the genus *Bullopora* (see above), the very rich material now available shows that this was a misinterpretation caused by diagenetic alteration of the test.

Juvenile specimens had the ability to bore facultatively into hard substrates. Imperforate walls do not exclude this habit, since most foraminifers are partly surrounded by ectoplasma, and pseudopodia are not necessarily restricted to the area of the opening of the test. The extant facultatively boring foraminifers *Rotaliammina* and *Siphotrochammina* exhibit an agglutinating, non-canaliculate, i.e. imperforate, test (Vénec-Peyré 1987, p. 207; 1988). Other features of these two genera parallel the *Troglotella* example. Compatible are the very thin walls and the reduction of wall formation in juvenile chambers (occasionally resulting in proteinous walls only, cf. Vénec-Peyré 1987; Loeblich and Tappan 1988). *Siphotrochammina* also exhibits a smooth outer surface. In contrast with *Troglotella*, both extant genera exhibit a trochospiral test which is a characteristic feature of the superfamily Trochamminacea.

The fact that *Troglotella* is imperforate may explain why the boring activity of the taxon is restricted to the juvenile stage (Text-figs 6–8; Pl. 2, fig. 5). At later stages the pseudopodia, which are more common around the opening in imperforate foraminifers, may not have reached down to the early ontogenetic chambers and hence could not further enlarge the bore hole, given the elongate shape of *Troglotella*.

The very thin character of the wall may have demanded further protection from enemies and elevated water energy, which may have been achieved either by occupying *Lithocodium* chambers or by a boring life-style. From the modern examples it is known that agglutinating foraminifers with a boring life-style use boring particles for wall formation (Vénec-Peyré 1987, p. 210).

Functional interpretation of morphology in foraminifers is debatable. Protection is certainly important but is only one function of the test. Among other explanations for test formation are the maintenance of protoplasma shape and cell organization without waste of energy (cf. Vogel and Gutmann 1988; Culver 1993). Excretion of calcareous skeletons may also serve to remove the cell toxin calcium (cf. Simkiss 1977). Consequently, test characteristics of boring foraminifers are rather variable. Extant *Planorbulinopsis parasita* (Banner 1971, termed '*P. parasitica*' in Loeblich and Tappan 1988) and some others exhibit thick walls (cf. Smyth 1988), by using drilled particles for test formation. The reason for drilling is, however, normally not to produce particles for test formation, since dissolved calcium carbonate is abundant in warm, shallow marine environments. On the other hand, *Troglotella* might have had problems in calcium carbonate availability within the test of living *Lithocodium* due to lacking direct contact with sea water (see below).

A partial to complete adaptation of the growth form of *Troglotella* to the morphology of *Lithocodium* chambers is apparent in almost all specimens (e.g. Pl. 1, fig. 3; Text-figs 1–2, 6). Particularly characteristic is the irregular growth of *Troglotella* tests towards, and sometimes even into, the alveoli of *Lithocodium* (Pl. 1, fig. 3; Text-fig. 1). Many adult *Troglotella* exhibit a very irregular shape due to decreasing space availability, and completely mimic the internal shape of *Lithocodium* chambers. In one example, the roof of a *Lithocodium* chamber was lifted off, but it is not clear whether this was caused by the growth of *Troglotella* or by external erosion (Text-fig. 6).

Comparison with other fossil organisms

In cases where *Troglotella* developed a very irregular adult growth form, it may show astonishing similarity to the enigmatic organism *Bacinella irregularis* (Pl. 1, fig. 5), which is commonly associated with *Lithocodium*, or with phrenotheca-like structures, respectively (see above). Since, in the Triassic and Cretaceous, and more rarely also in the Upper Jurassic, bacinelloid structures may also occur within the chambers of *Lithocodium*, confusion with very irregular *Troglotella* specimens could occur, particularly if the *Troglotella* is not completely preserved (e.g. Text-fig. 4). However, better preserved *Troglotella* specimens show that there is a clear, unconfusable morphological separation between the two taxa. Diagnostic are micrite threads crossing at right angles, which never occur in *Troglotella*.

The Triassic forms of the fusulinid genus *Endothyranella*, particularly *E. wirzi* (cf. Bucur *et al.* 1994, pl. 14, fig. 2), exhibit close similarities to *Troglotella*, both in their wall structure and general

growth form. According to Loeblich and Tappan (1988), the attribution of the Triassic forms to the Carboniferous representatives of the genus is doubtful.

Troglotella shows some similarity to *Cheilosporites tirolensis* Wähner, which, according to Senowbari-Daryan (1980*a*), represents a sphinctozoan coralline sponge, but which also has been interpreted as a foraminifer (Fischer 1962). Similarities comprise general growth form, segmentation into chambers and the partial cryptic life style of *Cheilosporites*. However, differences between the two are more obvious. *Cheilosporites* is ten times larger than *Troglotella* and shows an indistinct central canal which accounts for its attribution to the sphinctozoan sponges.

Substrate relation and the boring activity of Troglotella

The most common occurrence of *Troglotella incrustans*, which is restricted to the Upper Jurassic, is within the chambers of *Lithocodium*. Such specimens of *Troglotella* were facultative borers during the juvenile growth stage when attacking the substrate of *Lithocodium* (Text-fig. 6; Pl. 2, fig. 5), since *Lithocodium* does not form a basal wall. *Lithocodium* is never bored by *Troglotella*. Later growth stages encrust the bottom of the *Lithocodium* chambers, by developing the typical irregular growth. Occasionally, different specimens of *Troglotella* occupied one single *Lithocodium* chamber. Less commonly, *Troglotella* occurs outside *Lithocodium*, where it bored oncoids or bioclastic cortoids, and rarely also corals. In these cases, the last chambers extrude from the borehole and encrust their surface.

Wernli and Fookes (1992) noticed the occurrence of *Troglotella* within perforations, but excluded the idea of boring activity for *Troglotella*, due to the imperforate nature of the test which would prevent ectoplasma reaching the apex of the test where the supposed boring site had to be situated. In our opinion, this is not a sufficient argument since ectoplasmatic pseudopodia of foraminifers may reach lengths of up to three or more times the diameter of the test (Haynes 1981, p. 31), and therefore etching activity leading to boreholes seems not to be a problem even for imperforate foraminifers. This is corroborated by the existence of modern boring imperforate foraminifers (see

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EXPLANATION OF PLATE 2

Fig. 1. *Lithocodium* with chambers of *Troglotella* (left arrow) and phrenotheca-like structures (right arrow). Thin section AM I 2; Amaral Formation, late Kimmeridgian; Amaral ridge near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 23.

Fig. 2. *Lithocodium* specimen in which the diameter of chambers and alveoli is increasing from juvenile chambers (below) to adult chambers (above). The chambers are partly occupied by *Troglotella*. Thin section CH VII 1; Amaral Formation, late Kimmeridgian; Moinho da Chã near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 31.

Fig. 3. A thin bivalve shell is partially dissolved in places where overgrown by *Lithocodium*. Some chambers of *Troglotella* are also visible. Thin section 86/26.2.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; × 23.

Fig. 4. *Lithocodium* nodule; the chambers are occupied by *Troglotella*. Thin section CH VII 1; locality as in fig. 2; × 26.

Fig. 5. *Troglotella* occupying a chamber of *Lithocodium* (in tangential section), boring in a coral septum during juvenile stage. Thin section ALQ 12; Ota Limestone, 'middle' to late Kimmeridgian; Alenquer, Lusitanian Basin, Portugal; × 23.

Fig. 6. The microgranular and imperforate wall structure of *Troglotella* (lower arrow) and *Lithocodium* (upper arrow). M I 6B, scanning electron micrograph; Amaral Formation, late Kimmeridgian; Mata near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 670.

Fig. 7. A minute cryptic foraminifer with a very thin wall, occupying a chamber of *Alveolina* sp. The latter clearly reacted to the infestation by enlarging the infested chamber. Thin section ALV 1; Alveolinid limestone, middle Eocene; Criales near Villarcayo, Villarcayo Basin, Cantabria, northern Spain; × 50.

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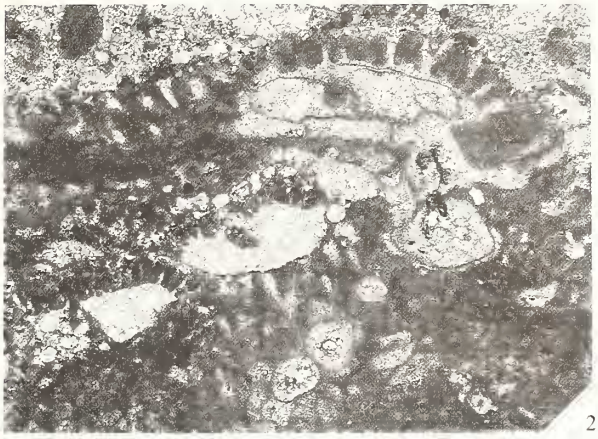
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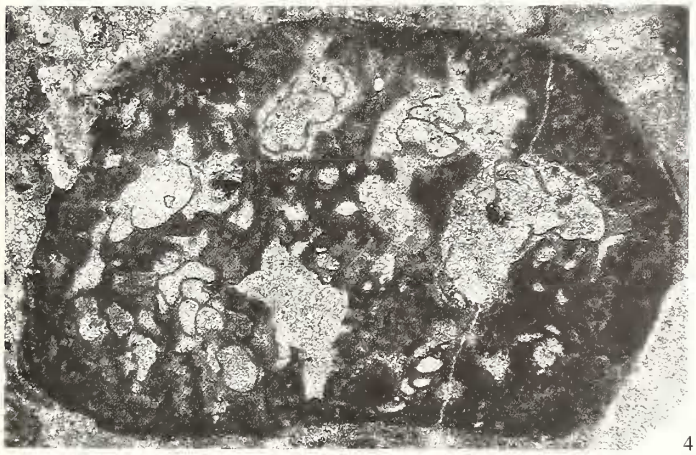
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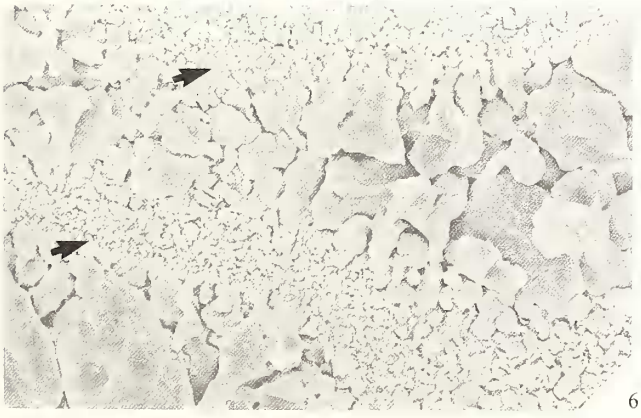
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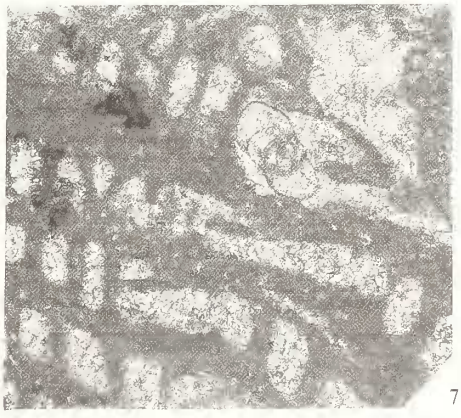
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SCHMID and LEINFELDER. *Lithocodium-Troglotella* foraminiferal consortium

below). Given the high tendency of *Troglotella* to exhibit morphological variation, the constant shape of the juvenile stage would be puzzling, if pre-existing cavities were passively occupied. Also, the lack of any space between the borehole and the test, as well as the constancy of the juvenile, seven to eight chamber arrangement, positioned perpendicularly to the substrate, substantiates the idea of the well developed boring abilities of the young foraminifer. The adult foraminifer had to change to a different life-style from the eighth chamber onwards. However, it must be emphasized that boring activity was facultative, and, given suitable shelter in a pre-existing larger cavity (i.e. particularly within a *Lithocodium* chamber) the boring activity was often suppressed.

Boring activity in other foraminifers

The boring activity of both agglutinating and rotaliid foraminifers is described comprehensively by Vénec-Peyré (1987). Other reports of boring foraminifers are from Banner (1971), Matteucci (1974), Baumfalk *et al.* (1982), Alexander and Delaca (1987), Smyth (1988), Cherchi and Schroeder (1991, 1992) and Vénec-Peyré (1993). Todd (1965) and Delaca and Lipps (1972) focused on *Rosalina* which is able to etch its substrate strongly, e.g. bivalve shells. Boring foraminifers generally etch and partly dissolve their calcareous substrate by means of their pseudopodia. Complete dissolution is not necessary, since loosened parts can be mechanically removed or, in the case of agglutinating foraminifers, even incorporated in the test. Pseudopodial etching activity may also cause thin, lateral channels (Banner 1971).

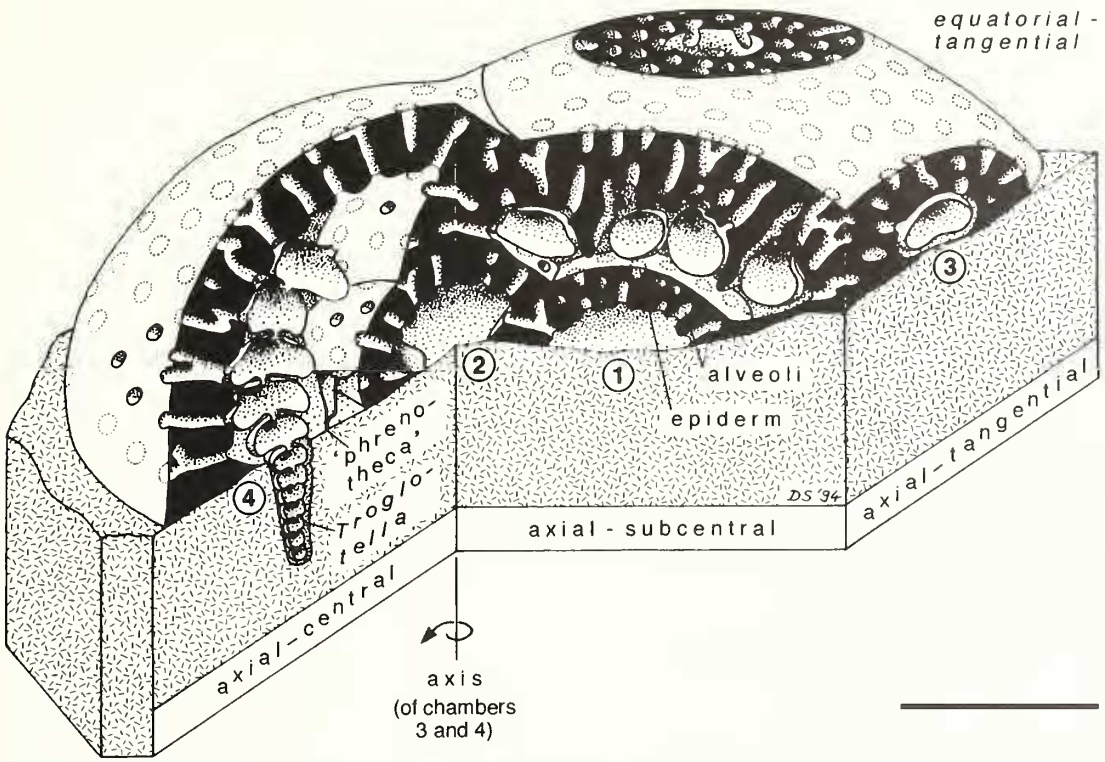
The first boring foraminifer described from the Upper Jurassic is *Troglotella incrustans* (see above) but, recently, another Upper Jurassic boring foraminifer has been described by Plewes *et al.* (1993). The form is known as *Globodendrina monile* and produces a globular hole with a series of radiating etched canals and a small agglutinated chimney rising from the surface around the hole. Therefore, this boring foraminifer differs clearly from *Troglotella*.

Examples of foraminifers boring into other foraminifers are rare. The extant miliolid *Alveolinella* is occasionally bored by the rotaliid *Planorbulinopsis* (Banner 1971). Baumfalk *et al.* (1982) described *Talpinella*, a rotaliid foraminifer from the Cretaceous, boring within tests of *Orbitoides*. *Talpinella* exhibits an early involute growth, whereas chambers increase rapidly in size and become irregular during later growth. This is a clear parallel with *Troglotella*. A major difference is, however, that *Talpinella* destroys the chamber walls of *Orbitoides*, something which has never been noticed in *Troglotella*. Another small foraminifer has been found boring into *Paleodictyoconus*, a Cretaceous foraminifer (Cherchi and Schroeder 1992).

LIFE STRATEGY OF THE *LITHOCODIUM-TROGLOTELLA* CONSORTIUM

The unique relationship between *Lithocodium* and *Troglotella* deserves special attention. In the Upper Jurassic, almost all *Lithocodium* specimens are found infested by *Troglotella*. On the other hand, *Troglotella* may occur rarely without *Lithocodium*.

Interpretation of the Upper Jurassic *Lithocodium-Troglotella* consortium is difficult, since apparently no direct modern counterparts exist. Partial modern analogues are foraminifers housing algal symbionts or parasitic heterotrophs (amongst which even foraminifers are known), commensal foraminifers in sponges, parasitic foraminifers in bivalves, foraminifers boring dead substrates, and foraminifers living cryptically in dead algal filaments as well as in other dead foraminifers. In the following, we will discuss the various possibilities of the heterotypic *Lithocodium-Troglotella* interrelationship and propose the most likely interpretation. The interpretation has to focus particularly on the following features: (1) the early boring stage of *Troglotella*; (2) the later irregular growth form of *Troglotella*, with *Troglotella* chambers normally paralleling the irregular inner surface of *Lithocodium* chambers; (3) the abundance of *Troglotella* within *Lithocodium*; (4) the occasional occurrence of *Troglotella* without *Lithocodium*; (5) the imperforate and multilayered character of *Lithocodium*; and (6) the occurrence of *Lithocodium* without *Troglotella*, particularly in material older or younger than Late Jurassic.



TEXT-FIG. 7. Reconstruction of *Lithocodium*, occupied by some specimens of *Troglotella*. 1–4 = succession of chambers of *Lithocodium*. In subcentral or tangential section, where connections between the chambers of *Troglotella* are not visible, the bubble-like chambers may resemble algal sporangia. Scale bar represents 1 mm.

Exclusion of post-mortem infestation of Lithocodium *by* Troglotella

Dead *Lithocodium* tests would have provided rather large cavities for the settlement of *Troglotella*. *Troglotella*, with its thin, fragile test would be perfectly sheltered and could occupy waters which would be too agitated for a free life style. *Hospitella*, a modern, probably allogromiid, foraminifer with imperforate, chitinous walls lives in the chambers of other, most probably dead foraminifers (cf. Loeblich and Tappan 1988, p. 17, pl. 10, fig. 3). In Upper Jurassic material (Birmensdorf beds, Oxfordian), Gaillard (1983, p. 214, text-fig. 99) identified the foraminifer *Tolypammina vagans* encrusting the inner wall of a chamber of the foraminifer *Bullopora tuberculata*.

As *Lithocodium* represents an imperforate foraminifer, the embryos or zygotes of *Troglotella* could have entered the empty tests only through the cribrate opening of the final chamber or through damaged walls. If *Troglotella* dwelt only occasionally within *Lithocodium*, it could be readily interpreted as post-mortem infestation. However, even in thick, multilayered *Lithocodium* crusts, most or all chambers are occupied by *Troglotella*, which makes post-mortem settlement most unlikely (e.g. Pl. 1, figs 2–3). If infestation had happened after the death of the entire *Lithocodium* crust, both settlement paths and flow of nutrient waters would be strongly hindered. Only if *Troglotella* could feed on decaying *Lithocodium* material, would nutrition appear feasible. However, in this case, the chambers would still be partially blocked and infestation of nearly all *Lithocodium* chambers would not be possible. Only a repetitive process of growth, death and infestment of *Lithocodium* would explain the occurrence of larger *Lithocodium* colonies with *Troglotella* in all chambers, an assumption which is most unlikely. Additionally, there would be no reason for the boring activity of *Troglotella* in its early ontogenetic stages. Moreover, phrenotheca-like structures, crossing the chambers and produced by *Lithocodium* are common in Triassic and Cretaceous

Lithocodium specimens (see below), but much rarer in Upper Jurassic ones. Although formation of phrenotheca-structures was possible in the Late Jurassic, its rarity shows that chambers were occupied by *Troglotella* prior to their possible time of formation, i.e. during the lifetime of *Lithocodium*.

The nature of coeval existence of Lithocodium *and* Troglotella

Although the coexistence of both foraminifers seems plausible, the kind of interrelationship is difficult to interpret.

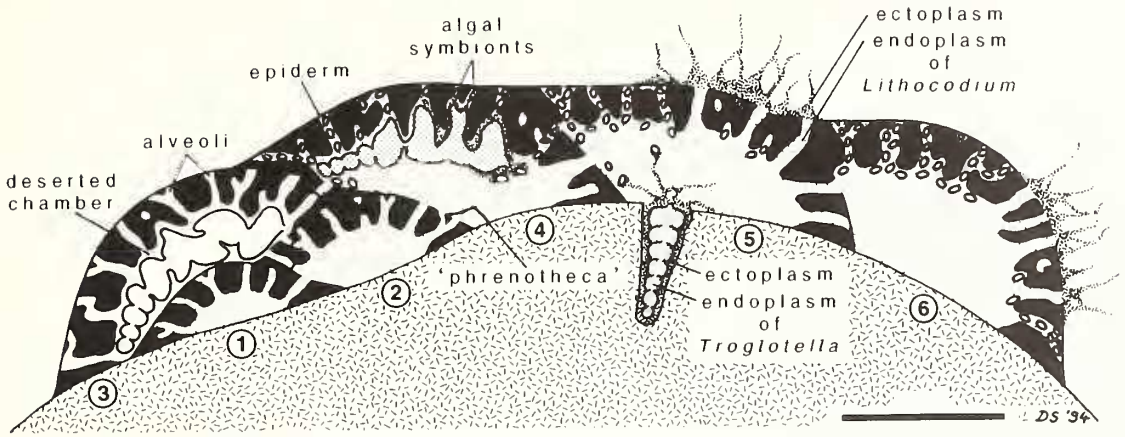
Cibicides refulgens is a modern foraminifer which lives epizoically on bivalves (Alexander and Delaca 1987). It bores the shell in order to obtain nutrition from the mantle cavity and thus exhibits a parasitic mode of life. Similarities with juvenile, boring specimens of *Troglotella* are apparent. Wetzel (1953) described *Bullopora parasitica* from the Middle Jurassic as an endoparasite within bivalves. The modern foraminifer *Planorbulinopsis parasitica* is considered as an endoparasite of another foraminifer (Banner 1971). Unlike *Troglotella*, the modern parasite does not, however, occupy almost the entire chamber space of the host. Loeblich and Tappan (1988, pl. 154, figs 7–8) figured a modern specimen of *Textulariella*, a genus with a wall structure similar to that of the loftusiaceans, in which several chambers are infested by a minute, spirally coiled foraminifer. Although this infestation is not mentioned in the text it might represent commensalism.

In the fossil examples, a parasitic life style for foraminifers living within other foraminifers is indicated either by the severe destruction or by the growth reactions of the host. Some examples for such an interpretation exist. Baumfalk *et al.* (1982) considered the Late Cretaceous boring foraminifer *Talpinella*, which lived within *Orbitoides*, as possibly parasitic. This interpretation was based on the fact that *Talpinella* perforated the chamber walls around the proloculus. According to the authors, there is no obvious penetration of the outer *Orbitoides* chambers and the partial destruction of foraminiferal hardparts excludes a post-mortem or a symbiotic/commensal life-style. A parasitic life-style is, furthermore, substantiated by the fact that *Talpinella* is not known outside *Orbitoides*.

We have detected a second example of a probable foraminiferal parasite living within another foraminifer from the Tertiary of Spain (Pl. 2, fig. 7). Here, a minute cryptic foraminifer with a very thin wall grew in a chamber of *Alveolina* sp. The latter clearly reacted by modifying and enlarging the infested chamber. The supposed endoparasitic foraminifer is involutely, probably planispirally coiled and has a dark, imperforate wall. As, to date, we have only one thin section specimen of this foraminifer, no taxonomic description can yet be given.

No damage or growth reaction related to the infestation by *Troglotella* is obvious in *Lithocodium*. If *Troglotella* was an endoparasite feeding on the *Lithocodium* endoplasma, it should have had severe effects on the host, particularly because almost the entire chamber space of the host would have been occupied, which contrasts with the modern and fossil examples of foraminiferal parasites within foraminifers given above. It may be argued that the large size of *Troglotella* does not unequivocally exclude a parasitic life style, but may have triggered *Lithocodium* to build rapidly new chambers. However, *Troglotella*-hosting *Lithocodium* grew to a considerable size, indicating an extended life time with healthy growth. The association was, moreover, very successful throughout the entire Late Jurassic. Given the generally high repair capacities of foraminifers, it seems unlikely that, for about 20 million years, *Lithocodium* would not have developed protective mechanisms, such as shutting-off infested chambers by closure of connective pores or formation of additional walls such as phrenotheca or the ability to digest the intruder, if *Troglotella* was a dangerous parasite. In fact, phrenotheca are tentatively interpreted in Text-figure 8 to have served partly to shut off chambers which had been deserted by *Lithocodium* for some reason, but this method was obviously not meant to prevent infestation by *Troglotella* generally.

On the other hand, virtually no evidence exists to suggest a symbiotic relationship between the two foraminifers. A variety of advantages is obvious for *Troglotella* when it lives within *Lithocodium* (see below), but no apparent advantages exist for *Lithocodium*. Theoretically, the



TEXT-FIG. 8. Reconstruction of the living *Lithocodium-Troglotella* consortium (axial section; algal symbionts not to scale). 1–6 = succession of chambers of *Lithocodium*. Phrenotheca-like structures are interpreted in this figure to have served partly to shut off chambers deserted by *Lithocodium* protoplasm. Scale bar represents 1 mm.

autotrophic symbionts of *Lithocodium* could have produced too much oxygen, endangering oxidation of plasma which could be neutralized by oxygen uptake of *Troglotella*. However, more plausible in this case would be that *Lithocodium* controlled the degree of oxygen production by partial ejection of symbionts, whereas direct digestion of surplus symbionts is thought to be rare (Murray 1991, p. 11). Symbiotic relationships between modern foraminifers and unicellular algae (symbiotic dinophyceans = 'zooxanthellae', symbiotic chlorophyceans = 'zoochlorellae', diatoms or rhodophyceans) are common (for comprehensive reports see Leutenegger 1984; Lee and Anderson 1991; Murray 1991).

Obviously, the infestation of *Lithocodium* by *Troglotella* did not greatly bother the host. Hence, the most likely interrelationship between *Troglotella* and *Lithocodium* was commensal, possibly with only a slightly parasitic effect. Text-figure 8 gives an interpretation of the relationship between both foraminifers. The following stages in the life cycle of *Troglotella* are thought to have occurred.

1. Infestation of *Lithocodium*. Probably by chemotaxis, sexually produced gametes settled on the ectoplasma of *Lithocodium* and were transported into the endoplasma. According to Kremer (1994), potential algal symbionts are generally recognized by their hosts by means of signal molecules and surface features, thus preventing digestion. The same mechanism may have prevented digestion of *Troglotella*.
2. Early growth stages. *Troglotella* attached itself to the floor of the *Lithocodium* chamber (i.e. normally the roof of the underlying chamber, or the *Lithocodium* substrate). If settling on the substrate, it commonly exhibited an early boring stage, either to produce material for test formation, to obtain nutrients from the substrate, to anchor itself within the flowing cytoplasma, or to create additional space (or a combination thereof).
3. Later growth stages. If *Troglotella* fed on the endoplasma of *Lithocodium*, it would not have been necessary for it to develop the irregular form of its adult stage. The rapid growth of *Troglotella*, particularly into the thin-walled alveoli of *Lithocodium* (i.e. into the presumed site of accumulation of autotrophic symbionts), rather suggests that *Troglotella* fed directly on these symbionts or their synthesized products. According to Lipps (1983, p. 339), permanently attached foraminifers, like *Troglotella*, are passive herbivores, which feed on bacteria and algae. In modern foraminifers, symbiotic algae may appear in great numbers. This explains why *Lithocodium* had only minor

disadvantages and could flourish despite the *Troglotella* infestation. The *Lithocodium* endoplasma was successively displaced by the growth of *Troglotella*, urging *Lithocodium* to form a new chamber. Probably, this lack of space was not too precarious, as Severin and Lipps (1989) were able to show that the living large foraminifer *Alveolinella quoyi* can only fill an average of 39 per cent. of its chamber space with protoplasm.

4. Reproduction. During asexual reproduction of *Lithocodium*, *Troglotella* embryos or gametes possibly already infested *Lithocodium* embryos and thus propagated. This would be the same mechanism which symbiotic algae use to pass over from parent individuals to new foraminifers (Röttger 1972; Hottinger 1982). Symbionts and, presumably, commensals cannot be passed over during sexual reproduction of gametes due to the very small size of the gametes (Leutenegger 1984). The products of sexual reproduction have to acquire their symbionts anew. This is one reason why large, symbiotic foraminifers largely reduced sexual reproduction in favour of the dominating asexual reproduction (cf. Röttger and Schmaljohann 1976; Hottinger 1983, text-fig. 3; Murray 1991, p. 11).

Reports on commensal foraminifers are rare. Voigt and Bromley (1974) describe a commensal association between agglutinating foraminifers (*Placopsilina* and *Bdelloidina*) and the papillae of clionid boring sponges from modern and Cretaceous examples. Probably, the foraminifers took advantage of the nutrient current produced by the propelling activity of the choanocyte flagellae. To our present knowledge, there are no modern examples of commensal foraminifers living within other foraminifers, although Le Calvez (1947) reported a partly comparable example in the case of the foraminifer *Fissurina*, which captures granules from the pseudopodial network of *Discorbis* for its own nutrition. On the other hand, looking at a totally different group such as the ants, numerous examples of symbiotic, commensal and parasitic relationships with various other insects have been identified (cf. Dumpert 1978), seemingly even more astonishing than the one recorded here.

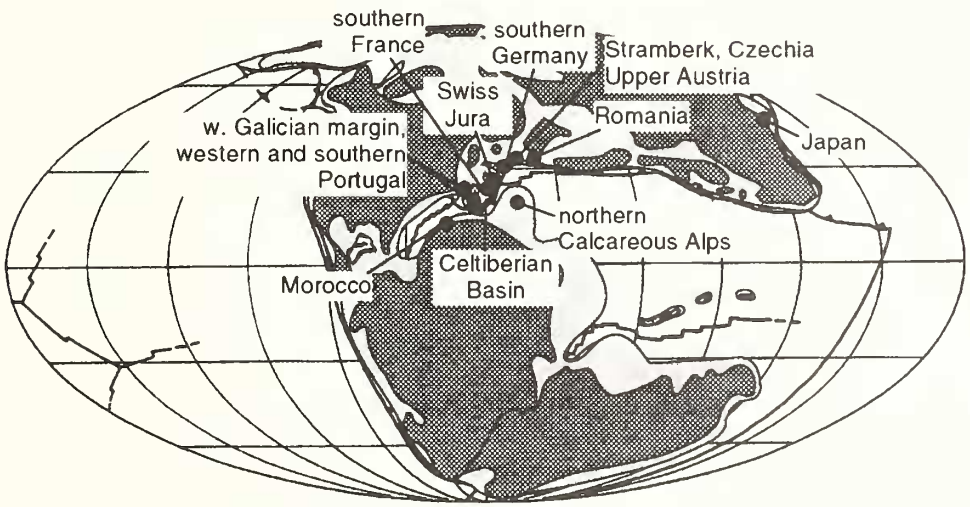
Troglotella occurs occasionally without *Lithocodium*, though it has to be taken into account that *Lithocodium* may still be present, but remains unrecognized (in tangential sections where the typical alveolar structure is barely visible). This does not exclude a commensal life of *Troglotella* inside *Lithocodium*, since even symbionts within foraminifers may also occur free-living. For instance, actively swimming dinoflagellates can apparently be attracted by foraminifers and used as symbionts by them (Ross 1972). However, the interpretation that *Troglotella* fed on autotrophic symbionts of *Lithocodium* or their products raises the question as to the nutrition of the occasional *Troglotella* specimens living outside *Lithocodium*. As has been mentioned above, these specimens always exhibit an early boring stage. In most cases, they attacked oncoidal nodules formed by cyanobacteria. They were also observed to have attacked solenoporacean red algae or *Marinella lugeoni*, a close relative of the coralline red algae (Leinfelder and Werner 1993). In the cases of attacks on bioclasts or corals, these specimens always exhibit a micritic rim caused by microbial borers, including cyanobacteria. This leads to the assumption that *Troglotella* outside *Lithocodium* may also have fed on autotrophic organisms or their products. The boring stage of these specimens can be interpreted as the result of the need for better protection, while the more regular, thicker chambers of the late, adult growth stage show that in cryptic specimens a more irregular, thin-walled, often barely visible, chamber clearly is the result of cavity outlines and the better protection available. Therefore, it must be concluded that there were not two different species or subspecies of *Troglotella*, but rather, that *Troglotella incrustans* exhibited wide intraspecific, ecological growth variation.

COMPARISON WITH *LITHOCODIUM* FROM OTHER STRATIGRAPHICAL LEVELS

Our description, taxonomic attribution and interpretation of the life habit of *Lithocodium aggregatum* is based on rich Upper Jurassic material. However, all figured Cretaceous specimens, including the original material of Elliott (1956), appear to be identical with the Upper Jurassic material. Judging from figured Triassic specimens, again, no apparent differences exist. Therefore,

we synonymize the entire material from *Lithocodium aggregatum*, although a re-study of the very widely distributed Triassic and Cretaceous material was not performed. However, in particular the original material of Elliott is abundantly figured, so that our conclusion seems to be substantiated at least for the Cretaceous forms.

All *Lithocodium* occurrences are clearly from warm, shallow, tropical to arid low-latitudes, exclusively from coral reef and lagoonal settings. The earliest occurrences are known from the Anisian of the Southern Alps (Bechstädt and Brandner *in* Senowbari-Daryan *et al.* 1993, p. 230). Particularly widespread in the Northern Calcareous Alps are Norian to Rhaetian occurrences (e.g. Zankl 1969; Flügel 1972; Kuss 1983; Matzner 1986). South Alpine (Lakew 1990) and Greek occurrences (Schäfer and Senowbari-Daryan 1983) of the same age are known as well. To our present knowledge, no forms of Early and Middle Jurassic age are recorded, which partly appears to be an effect of the lower abundance of reefs at this time (cf. Stanley 1988; Leinfelder 1994*b*), and partly due also to lack of investigation. It was particularly the Late Jurassic which brought an enormous spreading of *Lithocodium*, from the Atlantic to central and southern Europe, Northern Africa, and Japan (Text-fig. 9, also for references).



TEXT-FIG. 9. The distribution of *Lithocodium* during the late Jurassic, extending from Morocco (Hüssner 1985), the western Galician margin (Dupeuble *et al.* 1987), western and southern Portugal (Lusitanian Basin: Ramalho 1971; Leinfelder 1989; Algarve Basin: Leinfelder *et al.* 1993), the Celtiberian Basin (Fezer 1988; Wnendt-Juber 1990), southern France (Bouroullec and Deloffre 1968; Bernier 1984; Bodeur 1992), the Swiss Jura (Bolliger and Burri 1970), Southern Germany (Swabian Alb: Leinfelder *et al.* 1994, Franconian Alb: Barthel *et al.* 1971), Stramberk/Czechia (Eliasova 1981), Upper Austria (Hofmann 1993), Romania (Herrmann *in* Leinfelder *et al.* 1994) and the northern Calcareous Alps (Steiger and Wurm 1980; Darga and Schlagintweit 1991) to Japan (Endo 1961). World map from Scotese *et al.* (in press), simplified.

Cretaceous forms are also widely distributed in areas where reef or platform growth persisted, e.g. Texas (Johnson 1968*a*), Spain (Cherchi and Schroeder 1985), France (Jaffrezo 1974), Italy (Praturlon 1964), the Middle East (Elliott 1956; Saint-Marc 1970; Connally and Scott 1985; Alsharhan 1987) and the Far East (Endo 1961; Mu 1986; Moussavian 1992).

The *Lithocodium-Troglotella* consortium does not occur throughout the long range of *Lithocodium*. Chambers of all *Lithocodium* outside the Upper Jurassic either are empty (i.e. spar-filled) or are crossed by irregular, bacinelloid phrenotheca-like structures. Although these latter structures may rarely occur within the Upper Jurassic material as well, the vast majority of chambers is occupied by the endocommensal foraminifer *Troglotella incrustans*. Since infestation of

Troglotella did not really complicate life for *Lithocodium*, except possibly in speeding up chamber development, it took from the middle Oxfordian to the late Tithonian (*c.* 20 My) for the commensal form to disappear. It remains unclear as to whether *Lithocodium* developed a defense mechanism or *Troglotella* became extinct through other processes.

CONCLUSIONS

Lithocodium aggregatum Elliott is a loftusiid foraminifer with an encrusting life habit, not a codiacean alga. Features diagnostic for its foraminiferan nature are partial coiling of the test, microgranular, imperforate wall with alveoli, ability to agglutinate particles and facultative occurrence of phrenotheca-like structures. This reinterpretation is based on Upper Jurassic material, but no obvious differences exist in the Triassic and Cretaceous material.

Lithocodium is a typical shallow-water organism from lagoonal and reefal, high energy marine settings. It contributes considerably to the formation of oncoids and microbial-biotic crusts. The strong dependence on shallow, hence illuminated, water and the ability to create up to 0·1 m large, several millimetre thick, intensively calcified crusts suggests, but does not prove, the existence of photoautotrophic symbionts. This is also supported by the existence of common alveoli which may have been the site for such possible endosymbionts. The fact that light enhances the calcification rates of symbiont-bearing foraminifers has been observed by several authors (Lee and Anderson 1991, p. 199).

In the Late Jurassic, *Lithocodium* chambers are almost always occupied by the cryptic, telamminid foraminifer *Troglotella incrustans* Wernli and Fookes. *Troglotella* is interpreted here as a facultative borer during its juvenile stage. This stage is represented by regular growth of seven to eight chambers, completely filling the borehole. Later growth stages may become very irregular and may occupy a large proportion of *Lithocodium* chambers.

Cross sections of adult *Troglotella* chambers within *Lithocodium* may appear subcircular or tube-like and were previously mistaken for calcified sporangia of the *Lithocodium*-'alga'. These were used, among other criteria, to establish the species *Lithocodium morikawai* Endo and *L. japonicum* Endo, which are consequently invalid. *Lithocodium* appears to represent a monospecific genus.

The almost exclusive occurrence of *Troglotella* within *Lithocodium*, as well as the occupation of all *Lithocodium* chambers even within thick crusts, together with the imperforate nature of the *Lithocodium* wall, excludes post-mortem settlement. A parasitic life habit for *Troglotella* is unlikely because of its large size and the lack of growth reactions of *Lithocodium*, which seems unaffected by the infestation of *Troglotella*. A commensal association is indicated by the fact that adult *Troglotella* chambers have a strong tendency to grow into the alveoli of the host. This may indicate that *Troglotella* fed on the supposed photoautotrophic symbionts of *Lithocodium* or their synthesized products. Such an interpretation is compatible with the rare occurrences of *Troglotella* outside *Lithocodium* chambers where it occurs with algal or cyanobacterial crusts. The boring stage of *Troglotella* outside *Lithocodium* is always developed which reflects the need for better protection and anchoring.

The foraminifer *Lithocodium aggregatum* and the enigmatic *Bacinella irregularis* are two clearly different taxa. They have similar environmental demands and may overgrow each other, but also occur independently. This precludes them being two different ecological varieties, or different tissue parts, of one single organism, as suggested by some authors. However, *Lithocodium* may develop phrenotheca-like partitions irregularly subdividing its chambers. These structures are 'bacinel-limorph' and may in part account for the confusion of *Bacinella* with *Lithocodium*.

The reinterpretation of *Lithocodium* as a loftusiid foraminifer is another example of microproblematical forms being attributed to an alga simply to avoid dealing with a problem, as already stated by Babcock (1986). A similar case is represented by the well known, enigmatic '*Tubiphytes*' *morronensis*, occurring in the Jurassic and Cretaceous, which is interpreted by Schmid (1995) as a probably symbiont-bearing miliolid foraminifer with a two-fold test.

Acknowledgements. Many thanks are due to Martin Nose, Günter Schweigert, Stuttgart, and Winfried Werner, Munich, for numerous discussions and additional material. We would also like to thank Martin Baumgärtner, Andreas Jonischkeit, Ralf Laternser and Michael Reyle, Stuttgart, for additional material and valuable suggestions. This study is a contribution to the Priority Program 'Global and regional controlling processes of biogenic sedimentation – Evolution of reefs' of the Deutsche Forschungsgemeinschaft (DFG-project Le 580/4). Financial support is gratefully acknowledged.

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Typescript received 1 August 1994
Revised typescript received 12 June 1995